

PATTERNS OF MORPHOLOGY AND RESOURCE USE IN NORTH AMERICAN DESERT RODENT COMMUNITIES¹

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ABSTRACT.— As is true of many assemblages of ecologically similar organisms, coexisting heteromyid rodent species differ conspicuously in morphology and in microhabitat affinity. These patterns are so common that their explanation represents a central problem of community ecology. In the case of desert rodents, two very different factors, predation and competition, have been advanced as the ultimate cause of the patterns. We outline the way in which each of these factors could produce observed community-level patterns and review the evidence for the action of each factor. We conclude that the "competition" hypothesis has more support at the moment, but that this is partly a result of the general lack of good experimental studies of predation in terrestrial vertebrate systems. We outline a general protocol for distinguishing the effects of predation and competition through careful examination of relationships between morphology, foraging and predator-avoidance abilities, and behavior. We think such "micro-ecological" analysis of the consequences of morphology holds much promise for improving our understanding of community-level patterns of morphology and resource use.

Among the basic concerns of community ecology is identification of factors that determine the number, relative abundances, and phenotypic attributes of coexisting species. Rodents of North American deserts were important in the development of this major sub-discipline of ecology, mostly through the work of several influential naturalists—among them Joseph Grinnell and C. Hart Merriam—who developed their ideas about limits to animal distributions in large part from observing small mammals in the western United States. Their ideas have subsequently been incorporated into a sophisticated body of mathematical theory, the recent development of which was stimulated primarily by G. Evelyn Hutchinson and Robert H. MacArthur (see MacArthur 1972, Hutchinson 1978). Desert rodents in general still figure heavily in community ecology, being widely used for testing general theories of community organization under field conditions. They are especially suitable for such studies because they are small, abundant, diverse, and easily captured in the field and observed in the laboratory, and because unrelated groups have independently colonized geographically isolated arid regions.

Our aim here is not to review exhaustively what is known about desert rodent communities, since several other authors have made recent contributions of this sort (Brown 1975, Rosenzweig et al. 1975, Brown et al. 1979). Instead, we will provide an updated overview of the general characteristics of these communities, discuss the alternative hypotheses that have been advanced to explain those characteristics, and outline the evidence that bears on the alternatives. Finally, we will suggest directions for further research. We will focus on the specialized seed-eaters of North American deserts because much less is known about other desert rodents, but we will attempt to indicate when observations from other dietary guilds or geographic regions fit the patterns we describe.

GENERAL PATTERNS

Natural History

The rodent fauna of North American deserts is dominated by members of the Heteromyidae, a New World family whose remarkable similarity to unrelated Old World and Australian desert forms is a textbook example of convergent evolution. Like jerboas,

¹From the symposium "Biology of Desert Rodents," presented at the annual meeting of the American Society of Mammalogists, hosted by Brigham Young University, 20–24 June 1982, at Snowbird, Utah.

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gerbils, and hopping mice, most heteromyids are primarily granivorous and can subsist without a source of free water. They are also nocturnal, live in burrows, and include both bipedal hopping (*Dipodomys*, *Microdipodops*) and quadrupedal bounding forms (*Perognathus*). A more complete analysis of morphological, behavioral, and ecological similarities among unrelated desert rodents can be found in Eisenberg (1975), Brown et al. (1979), and Mares (this volume).

Some of the convergent features of these groups, such as xerophytic physiology and burrowing habit, are clearly responses to the extreme temperatures and low rainfall that characterize deserts. Others, such as granivory, are probably indirect consequences of plant responses to frequent and unpredictable droughts. Many desert plants have adopted an "ephemeral" life history, in which they survive unfavorable periods as seeds or (less often) as underground storage organs (Noy-Meir 1973, Solbrig and Orians 1977); and the resulting pool of dormant seeds in the soil provides a relatively abundant and persistent food source for a variety of birds, rodents, and ants (Noy-Meir 1974, Brown et al. 1979). The significance of still other features of desert rodents, such as prevalence of bipedal locomotion, remains a matter of debate, but these features probably reflect constraints on predator avoidance or foraging strategies imposed by the physical structure of desert vegetation and soils (see Bartholomew and Caswell 1951, Brown et al. 1979, Thompson et al. 1980, Reichman 1981, Thompson 1982a,b).

Proximate Factors Affecting Abundance and Diversity

There is considerable evidence that individual reproductive success and population densities of rodents in North American deserts are limited by seed production of ephemeral plants, whose germination and growth is directly tied to the amount of precipitation falling during certain seasons (Noy-Meir 1973). Reproductive rates of individual rodents, as well as population densities, show extensive temporal and geographical fluctuations that are closely correlated with variation in precipitation (Brown 1973, 1975,

French et al. 1974, Brown et al. 1979, M'Closkey 1980, Petryszyn 1982, Munger et al., this volume). Casual observation of climatic correlates of rodent "plagues" in other regions suggests that this is probably true in all deserts (see references in Prakash and Ghosh 1975).

Species diversity seems to be influenced by several factors, the most obvious of which is habitat complexity (Rosenzweig and Winakur 1969, M'Closkey 1978). Positive correlations between diversity and habitat complexity are common in animal communities (MacArthur 1972, Schoener 1974, Hutchinson 1978), and occur because coexisting species usually differ in affinities for areas of particular topographic or vegetation structure. If it is sufficiently productive, an area that is structurally complex can be inhabited by several species, each of which specializes on a different microhabitat. Interspecific differences in microhabitat affinity appear to be characteristic of all desert rodent communities that have been examined (cf. references in Prakash and Ghosh 1975). Among heteromyids, the bipedal kangaroo rats and kangaroo mice are associated with sparse perennial vegetation and tend to forage in open microhabitats, whereas the quadrupedal pocket mice are associated with dense perennial vegetation or rocky areas and prefer microhabitats under tree or shrub canopies (Rosenzweig and Winakur 1969, Rosenzweig 1973, Brown and Lieberman 1973, Brown 1975, Price 1978b, Harris unpublished, Price and Waser 1983). This pattern also appears to occur in African deserts where bipedal jerboas are associated with open areas more than are quadrupedal gerbils (e.g., Happold 1975).

Several experimental studies indicate that vegetation structure influences not just the number of species in North American communities, but also the identities and relative abundances of those species. Rosenzweig (1973) altered a number of small plots by clearing shrubs from some and augmenting brush on others. These manipulations resulted in significant local shifts in species composition: *Perognathus penicillatus* increased in density on augmented plots and decreased on cleared plots, but *Dipodomys merriami* responded in the opposite way. Similarly, Price

(1978b) removed half of the small shrubs from 25 sites within a 3.2 ha area and found predictable increases in the density of *D. merriami*, the species that showed the most pronounced preference for foraging in open spaces. Furthermore, the magnitude of local changes in density of this species was correlated with the amount of shrub cover removed. After adding cardboard "shelters" between shrubs to experimental plots, Thompson (1982b) observed increased abundance of species normally associated with shrubs and decreased abundance of kangaroo rats. "Natural" temporal or spatial changes in vegetation appear to result in similar shifts in rodent species composition that can be predicted from knowledge of microhabitat preferences (Rosenzweig and Winakur 1969, Beatley 1976, Hafner 1977, Price 1978b, Price and Waser 1983).

Among habitats that are similar in structure, the number of rodent species increases with the amount and predictability of annual precipitation, which determines seed production as well as shrub density (Brown 1973, 1975, Hafner 1977, Brown et al. 1979). The most arid parts of the Colorado and Mojave deserts typically have only one or two species of heteromyids, whereas structurally similar but more productive areas in the Sonoran, Chihuahuan, and Great Basin deserts sometimes support as many as four or five species. As might be expected, average population densities and total rodent biomass also tend to be positively correlated with increased seed abundance, but it is less clear why species diversity should exhibit such a pattern. MacArthur (1969, 1972) showed that this correlation is expected of communities composed of species limited by a single resource. In such resource-limited systems, species that specialize on a subset of available resources can persist only when overall production is high enough to supply some minimal amount of the preferred subset during poor years. In unproductive regions, abundance of the appropriate resources may often fall below the threshold level, causing the consumer populations that depend on them to go extinct locally. Brown (1973) has proposed this explanation for geographic diversity-productivity correlations in heteromyid communities. A similar explanation would also account for

seasonal variations in species occupying given habitats (cf. Congdon 1974, Meserve 1974) and for species turnover between local habitats that differ in structure. There is not as yet sufficient evidence to evaluate rigorously these productivity-based explanations of species diversity, although they are consistent with results of one experimental study: artificial augmentation of seeds in a short-grass prairie enhanced local species diversity by inducing invasion of a specialized granivore, *Dipodomys ordii* (Abramsky 1978).

Brown (1973, 1975) has pointed out that historical factors, in addition to productivity and habitat structure, can influence the number of species in heteromyid communities. He found that geographically isolated sand dunes were inhabited by fewer species than would be expected on the basis of their productivity, and attributed this to decreased colonization rates of isolated "islands" of suitable habitat. Historical constraints have also been invoked to account for the low diversity of rodents in South American and Australian deserts (Brown et al. 1979).

Morphological Configuration of Rodent Communities

In addition to pronounced divergence in microhabitat affinities, a salient feature of heteromyid communities is that coexisting species differ in body size more than would be expected if communities were random assemblages of species (Fig. 1; Brown 1973, 1975, Brown et al. 1979, Bowers and Brown 1982). Such body size divergence is by no means unique to desert rodent communities; in fact, it is so ubiquitous that nearly constant size ratios among coexisting species have been given the name "Hutchinson's ratios," after the ecologist who drew attention to them (Hutchinson 1959, Horn and May 1977, Lack 1971, MacArthur 1972). Heteromyid communities are, however, one of the few cases for which observed size spacing has been shown to be statistically different from random null models (cf. Strong et al. 1979, Bowers and Brown 1982, Petersen 1982, Simberloff and Boecklen 1981). It is interesting to note that desert cricetids do not show size patterns typical of heteromyids, and that including the omnivorous and carnivorous

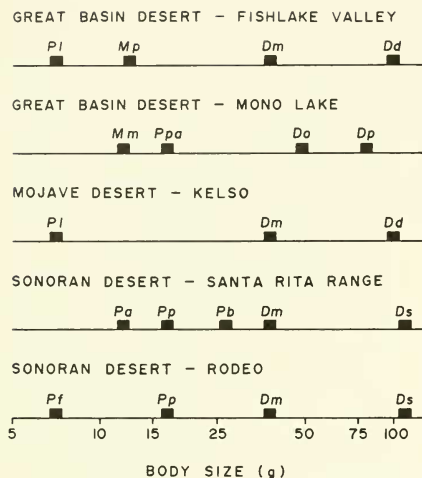


Fig. 1. Typical heteromyid rodent assemblages from three major North American deserts. The average body sizes of common species found at five sites are indicated by their position on the horizontal axis. P1 = *Perognathus longimembris*; Pf = *P. flavus*; Pa = *P. amplius*; Pp = *P. penicillatus*; Ppa = *P. parvus*; Pb = *P. baileyi*; Mm = *Microdipodops megacephalus*; Mp = *M. pallidus*; Dm = *Dipodomys merriami*; Do = *D. ordii*; Dp = *D. panamintinus*; Dd = *D. deserti*; Ds = *D. spectabilis*. Note that congeners of similar body size are not common at the same site. Data taken from Brown (1973) and Price (unpublished).

cricetids along with the heteromyids in a morphological analysis obscured patterns present within the granivore guild (Bowers and Brown 1982, Petersen 1982). There have been no studies of morphological structure similar to these for desert rodent systems in continents other than North America. This is unfortunate, because there are intriguing suggestions of size differences among coexisting gerbils in North Africa (Happold 1975:36) and among dipodids in the USSR (Naumov and Lobachev 1975:491).

Coexisting heteromyids differ in parameters of body shape related to locomotory gait as well as in size. Relative to quadrupedal forms, bipeds have elongated hind feet and tails, shortened vertebral columns, and reduced fore feet (Hatt 1932, Howell 1932). There is some association between shape and size; in general, bipedal forms are larger (12–150 g) than quadrupedal forms (7–40 g).

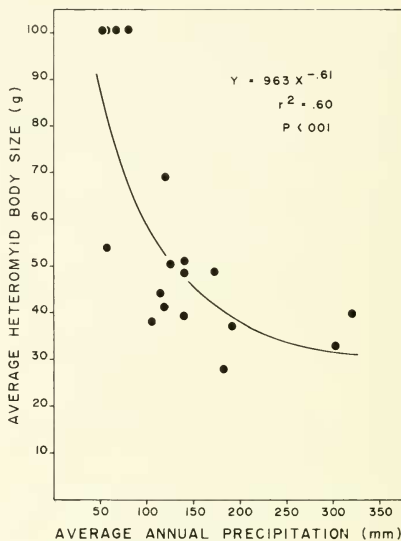


Fig. 2. Average body size of heteromyids resident on sand dunes that differ in annual precipitation, unweighted by relative species abundances. As species number decreases with decreasing precipitation, the smaller species drop out first. This causes a significant increase in average body size as productivity declines, until only the largest kangaroo rats remain on the most arid dunes. Data are from Brown (1973); the power fit shown on the figure is significant ($F_{1,16} = 24.43$; $P < .001$).

In addition to these within-community morphological patterns, there are striking geographical trends in body size for sand dune habitats. Figure 2 indicates that as species diversity declines along a gradient of decreasing precipitation, average size of heteromyids inhabiting sand dunes increases. This is not due to geographic variation in size within individual species, although such variation has been reported (Kennedy and Schnell 1978). Instead smaller species drop out first along the gradient, until only the largest species remain in the least productive regions. It remains to be seen whether similar patterns exist for other habitats.

PROPOSED EXPLANATIONS FOR THE PATTERNS

The Hypotheses

Two hypotheses have been advanced to account for the conspicuous interspecific diver-

gence in body size, shape, and microhabitat affinity that characterizes heteromyid rodent communities. The first proposes that these features reflect divergent predator avoidance strategies that have evolved because there can be no single "best" escape strategy in heterogeneous environments (cf. Rosenzweig 1973, Thompson 1982a,b, Webster and Webster 1980). An escape behavior that works well away from cover, for example, may be ineffective in dense brush either because shrubs impose physical constraints on movement or contain different types of predators. It is not difficult to imagine that morphology determines how easily an animal can be detected and which escape strategies it can use effectively. If each microhabitat requires a different escape strategy, then a particular morphology defines the relative risk associated with foraging in different microhabitats. The predation hypothesis can account for associations between heteromyid form and microhabitat if animals rank microhabitats on the basis of risk, and forage selectively in the safest areas. This would cause species differing in morphology to differ in their ranking and use of microhabitats. Predation could also interact with food availability to account for diversification of form within communities, if predation pressure restricts the microhabitats in which each species can forage efficiently, so that some microhabitats are initially utilized less intensively than others. In this case seeds would tend to accumulate in those microhabitats that are risky for resident species, and such microhabitats would eventually be colonized by species whose morphology and escape behavior allow their safe use.

The second hypothesis (cf. Brown 1975, Price 1978b, M'Closkey 1978) proposes that divergence in morphology and microhabitat affinity is the outcome of competition for seed resources. A predicted outcome of competition is divergence among competitors in use of limited resources, and in morphological and behavioral traits that influence the efficiency with which particular types of resources can be utilized (MacArthur 1972, Lawlor and Maynard Smith 1976). This hypothesis can account for observed microhabitat affinities if microhabitats differ in the types of seeds they contain or in the methods

required to harvest seeds, and if body size and shape influence the efficiency of harvest in a particular microhabitat. Under these conditions, animals can be expected to rank and utilize microhabitats on the basis of harvest rates.

Little progress has been made in determining the relative importance of predation and harvest efficiency in shaping characteristics of heteromyid communities, although authors often invoke one or the other factor exclusively to explain microhabitat preferences or morphological attributes (cf. Eisenberg 1963, Rosenzweig 1973, Brown 1973, Price 1978b, Thompson et al. 1980, Webster and Webster 1980, Reichman 1981, Thompson 1982a, b). The problem with treating these as alternative hypotheses is that both factors may influence foraging behavior. According to optimal behavior models (cf. MacArthur and Pianka 1966, Pyke et al. 1977, Werner and Mittelbach 1981), animals should rank microhabitats according to the fitness gain realized while using them. Because fitness gain is a complex function of resource harvest rates discounted by expected costs or risks, interspecific differences in microhabitat choice could come about if species differ in their abilities to harvest resources and/or to avoid physiological stress or predation in particular microhabitats. It is difficult to devise an experimental protocol that would directly distinguish the relative importance of harvesting efficiency and predator avoidance in determining microhabitat choice, since this requires that each factor be varied separately—and predation risk is not especially susceptible to effective manipulation.

Until direct experimental tests of the "predation" and "harvest efficiency" hypotheses can be devised, we feel the best way to begin evaluating their importance is to examine in detail the plausibility of the assumptions about morphology and behavior upon which they are based, and to scrutinize community-wide patterns for any that might be inconsistent with one or the other hypothesis. We will concentrate on such an analysis in the rest of this section.

Evidence for the Role of Predation

There can be no doubt desert rodents represent a major food source for a variety of

predators. In North America, hawks, owls, snakes, and carnivorous mammals have been reported to take rodents, and populations of all these predators are dense enough to represent a significant source of mortality (cf. Pearson 1966). The importance of predation as a selective agent is further suggested by widespread correspondence between pelage and substrate colors in desert rodents (Benson 1933, Dice and Blossom 1937). This substrate matching has evolved because visually hunting predators selectively attack individuals that contrast with their background (Dice 1945, 1947, Smith et al. 1969, Bishop 1972, Kaufman 1974).

Estimates of potential predation rates for kangaroo rats have come from experiments comparing disappearance rates of marked individuals whose hearing had or had not been impaired experimentally (Webster and Webster 1971). Thirty-three percent of normal and sham-operated animals disappeared within a month of being released, along with 78 percent of the deafened animals. Most of the latter disappeared during the dark phase of the moon. Although it is impossible to tell what part of the 33 percent loss of normal animals was caused by predation rather than dispersal, the 45 percent increment in loss of deafened animals suggests that predators may be a potentially important source of mortality, at least for unwary or weakened animals.

There is some evidence that rodents respond behaviorally to risk of predation, but it is mostly inferred indirectly from evidence relating light intensity to rodent activity, or to predator success. Dice (1945) observed that owls have difficulty detecting immobile prey at light intensities lower than about 7.3×10^{-7} foot-candles (values equivalent to that under dense foliage on a cloudy night). Although owls can also use hearing to locate active prey, it is reasonable to expect hunting success to be higher on moonlit nights, unless prey experience a correspondingly greater ability at high light levels to detect and escape from approaching predators. Webster and Webster's (1971) observation that deafened kangaroo rats disappeared primarily in the dark phase of the moon would suggest that light can help prey as well as predator. In any event, Blair (1943) noted that deer

mice exhibited reduced activity in the laboratory when light intensities exceeded levels typical of clear moonless nights. Similarly, Lockard and Owings (1974, but see Schroder 1979) reported reductions in visitation to feeding stations by free-ranging Banner-tailed Kangaroo Rats during periods of moonlight. Kaufman and Kaufman (1982) observed fewer kangaroo rats on standard nightly road censuses and observed more animals on shaded than unshaded sides of the road when the moon was up. Burt Kotler (pers. comm.) experimentally manipulated light levels in the field with lanterns and observed decreased foraging by desert rodents at seed trays when light levels approached those of bright moonlight. Although these authors concluded that overall kangaroo rat and deer-mouse activity is sensitive to risk of predation, there is no direct evidence that the effect of moonlight on activity has to do with predation risk. It is conceivable, for example, that animals avoid bright light simply because it is uncomfortable for dark-adapted eyes.

There is also little evidence that microhabitat use is influenced by predation risk. Dice (1947) found that artificial bushes reduced the number of deer mice taken by owls in experimental rooms, and Lay (1974) remarked that owls were less successful in attacking mice near an obstruction such as a wall; this leads one to expect that mice are safer in structurally complex areas. Blair (1943) did not note, however, that deer mice restricted their activity in the center of the room relative to low-risk areas near walls or the nest box when light intensities were high. Burt Kotler (pers. comm.) found that kangaroo rats spent a greater proportion of their time under shrubs when he had increased light levels experimentally with lanterns. Taken altogether, these studies suggest that light influences overall activity and microhabitat use, but the inference that these behavioral changes are responses to enhanced predation risk remains tenuous. Clearly, more experimental work needs to be done. It is especially important to determine the relationship between light intensity, microhabitat, and predation risk for different kinds of desert rodent.

Although there are interspecific differences in the ease with which rodents can escape detection or attack by particular predators, it is not known how these behaviors are related to differences in body size or shape. From the experiments of Dice (1947), Lay (1974), Kaufman (1974) and Webster (1962, Webster and Webster 1971), it appears that deer mice (*Peromyscus*) are much more vulnerable to owls than are kangaroo rats (*Dipodomys*) or gerbils (*Meriones*); the latter two groups often remained unscathed after a night's confinement in a bare room with a hungry owl. Several features of kangaroo rats have been related to their remarkable ability to avoid predators (Bartholomew and Caswell 1951, Webster 1962, Webster and Webster 1971, 1980). Their inflated middle ear cavities enhance sensitivity to the low-frequency sounds made by striking snakes and owls, and enlarged, dorsally placed eyes are sensitive to sudden movements in dim light. Kangaroo rats with either or both sensory modes intact readily avoid attack by leaping suddenly upward or backward out of reach of the predator. Elongated hind feet and tails appear to facilitate these maneuvers, which are effective for predators like owls and snakes that cannot easily change trajectory during an attack. Because deer mice lack ears specialized for detecting low-frequency sound as well as specialized anatomy to facilitate leaping, it is not clear whether they do not avoid owls effectively because they cannot detect them in time, or because they cannot use erratic leaping as an escape response. The former explanation seems more likely. Lay (1974) noted that *Peromyscus* made no attempt to escape owl attack until after they were captured, as though they were unaware of the predator's approach. He also noted that *Meriones*, which have enlarged auditory bullae like kangaroo rats but lack their extreme bipedal adaptations, could effectively jump or run out of the owl's way. Thus it appears that detection of predators is more critical for survival than leaping ability.

Although size apparently is important in determining prey choice by certain predators (cf. references in Hespeneheide 1975, Wilson 1975), it is not obvious how size influences net predation risk among desert rodents. In general, small predators are less efficient at

subduing large prey and therefore consume smaller prey on average than do large predators. In some animals, such as barnacles (cf. Connell 1975), an individual becomes immune to predation once it has grown to some threshold size. Large size in heteromyids may, therefore, confer some immunity from small predators on the one hand, but on the other could make them more conspicuous and desirable for larger predators, which would then concentrate their efforts on these preferred large prey.

It is unfortunate that nobody has compared predator escape abilities of pocket mice and kangaroo rats directly, because the former are often assumed to lack the kangaroo rat's facility in escaping predators. This assumption is based on differences in morphology between heteromyid genera that are qualitatively similar to differences between heteromyid and cricetid rodents as a whole. It may well be unwarranted. Webster and Webster (1975, 1980) have examined the morphology and sensory physiology of heteromyid ears. They calculate that ears of all three of the desert genera (*Dipodomys*, *Microdipodops*, *Perognathus*) have a theoretical best transmission of 94–100 percent of the incident acoustical energy reaching the outer ear. This theoretical efficiency is achieved by enlargement of the tympanic membrane in *Dipodomys* and *Microdipodops*, the two forms with inflated auditory bullae, whereas it is achieved by reduction of the stapes footplate in *Perognathus*. Actual sensitivity of *Dipodomys* and *Microdipodops* ears to low frequency sounds (less than about 3 k Hz) appears greater than that of *Perognathus*, judging from the sound intensity required to produce a 1 μ V cochlear microphonic (Webster and Webster 1980). This is to be expected from the relatively greater reduction in stiffness relative to mass of the middle ear apparatus that is achieved by using enlarged tympanic membrane rather than reduced ossicle mass to achieve overall auditory sensitivity. Although suggestive, these results are not conclusive because cochlear microphonics do not show actual auditory thresholds; behavioral studies will be necessary to determine to what extent the lower sensitivity of *Perognathus* ears actually impairs their ability to detect predators in nature

(Webster and Webster 1971). If there is a difference between pocket mice and kangaroo rats in susceptibility to predation it is more likely a function of sensory than locomotory capabilities. There is no evidence that pocket mice are substantially less able than bipedal forms to use erratic leaping to avoid predators, even though they use quadrupedal bounding for straightaway running at high speeds. Bartholomew and Cary (1954) observed that pocket mice are adept at erratic leaping, an observation anyone who has tried to catch an escaped pocket mouse can confirm. Whether this ability to escape human pursuers implies equal facility with natural predators is, of course, not known.

We conclude from this survey that predation has undoubtedly been of general importance in the evolution of some aspects of desert rodent behavior and morphology, but its role in promoting divergence among coexisting heteromyids in morphology and microhabitat use has yet to be elucidated.

Evidence for the Role of Competition

The case for an important role of competition is stronger, but is by no means complete. Munger and Brown (1981) recently have provided experimental evidence that heteromyids compete: removal of kangaroo rats results in increased densities of smaller granivorous, but not omnivorous, rodents in experimental enclosures. This is the most robust sort of evidence for the existence of resource-based interspecific competition (cf. Connell 1975). Although such experiments document the existence of competition, they can tell us little about the evolutionary consequences of this interaction for community-level patterns of morphology and microhabitat affinity.

The fact that seed availability limits reproductive success of individuals indicates that, like predation, competition must have represented a strong agent of natural selection, in this case for efficient seed harvest. Anecdotal evidence suggests that heteromyids are indeed efficient "seed-vacuuming machines." Lockard and Lockard (1971) found that *Dipodomys deserti* could accurately pinpoint the location of a one-gram packet of millet seed buried 20 cm in the soil. We have observed desert rodents routinely collecting

90–100 percent of millet seeds widely dispersed on the soil surface in a night's time (Brown, unpublished); and oats sprinkled near traps during a recent field trip to Kelso Dunes, California, were harvested from 120 of 150 traps by *Dipodomys deserti* (Price, pers. obs.). In the laboratory, we have clocked pouching rates of 16 millet seeds per second in *D. deserti* (Price, unpublished). Finally, Monson (1943) found that *D. spectabilis* harvested and stored an average of about 20 qts of seed per month during fall seed production. The question remains, however, whether interspecific differences in morphology imply differences in the kinds of seed resources that can be harvested most efficiently.

Because differences in body size are so pronounced among coexisting heteromyids, the search for correlations between size and foraging behavior has been intense. Brown and Lieberman (1973; see also Brown 1975, Brown et al. 1979, Bowers and Brown 1982) initially proposed that heteromyids of different size partition resources in part by eating seeds of different size. They sieved seeds taken from cheek pouches and found a positive correlation between body weight and average seed size as measured by the size of sieves in which seeds settled. (This is a measure of seed linear dimensions.) Lemen (1978) subsequently reanalyzed their samples using weight of hulled seeds as the measure of seed size (rather than weight of the seed, hulled or unhulled, as it was found in the pouch) and found no correlation between rodent weight and average weight of seeds taken. Laboratory feeding trials generally support Lemen's (1978) conclusion that body size differences do not reflect differences in seed size selection (Rosenzweig and Sterner 1970, Hutto 1978; but see Mares and Williams 1977).

We have recently improved on these studies by offering caged heteromyids wheat ground to different sizes, rather than an array of seed species that differ in size. This controls for confounding effects of taste preferences. We find no indication that large heteromyids prefer large seeds; if anything, *D. deserti* harvests more small particles than do smaller species (Fig. 3a, b; Price unpublished). Results of these laboratory experiments are substantiated by field studies of

heteromyid food habitats, which indicate that sympatric rodents eat largely the same seed species (Smigel and Rosenzweig 1974, Reichman 1975, O'Connell 1979, Stamp and Ohmart 1978). Differences in diet may reflect spatial differences in what seeds are available where the animals forage rather than intrinsic differences in what seeds are selected once they have been encountered (Reichman 1975, O'Connell 1979, M'Closkey 1980). This lack of apparent differences in seed preference is supported by results of a preliminary laboratory study (Figure 3c; Price unpublished), in which no pronounced interspecific differences in consumption of eight seed species were observed.

The discrepancy between results Brown and Lieberman (1973) obtained by sieving cheek pouch contents and those Lemen (1978) obtained by weighing is intriguing. We believe it is real, and that it may be the result of a body-size-dependent difference in heteromyid foraging behavior. Such a discrepancy could come about if larger heteromyids more commonly take seed heads from plants directly rather than gleaning dispersed seeds from the soil (the seed head would have a larger linear dimension than a single detached seed), or if the small cheek pouch volume relative to metabolic demands of smaller heteromyids (Morton et al. 1980) requires them to remove bulky husks from seeds before pouching them (a husked seed has a smaller linear dimension than an unhusked one). The former possibility could result in partitioning of seed resources, but the latter would not. In both cases, sieving would show a positive relationship between rodent and seed size, but weighing hulled seeds would not.

There are other respects in which body size could influence foraging choices made by heteromyids. Price (1981, 1982a) has developed a simple model of a heteromyid foraging on a patchy seed resource. The model predicts that because harvest rates, travel speeds, and metabolic costs are allometric functions of body size, the degree to which an animal will specialize on the most profitable patches should depend on its size. Until we obtain accurate estimates of model parameters for the heteromyid system, however, we will not be able to determine

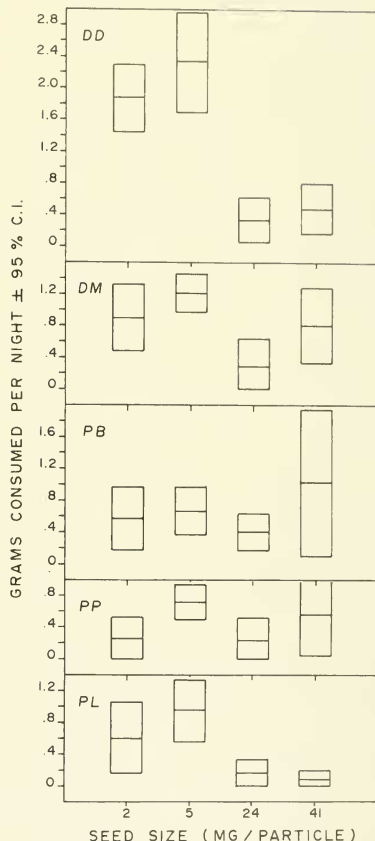


Fig. 3. Consumption of different sizes or species of seed by caged heteromyids having prior experience with the experimental food.

A. Animals were presented with equal weights of four size classes of ground wheat particles and left undisturbed to feed for a night. In the morning, remaining seeds were recovered by sieving and amounts of each size consumed determined by subtraction. Sample sizes were six runs for each rodent species. Abbreviations of specific names are as in Figure 1. MANOVA indicates a significant effect of species on consumption (Wilks' $L = .018$; $F_{16,37} = 7.65$; $P < .0001$), but discriminant analysis indicates the major interspecific difference is a simple effect of body size on consumption of all seed sizes ($\lambda = .22$), with a much less pronounced variation among species in the degree to which very large seeds are avoided ($\lambda = 2.4$). Notice that there is no correlation between body size and seed size selection.

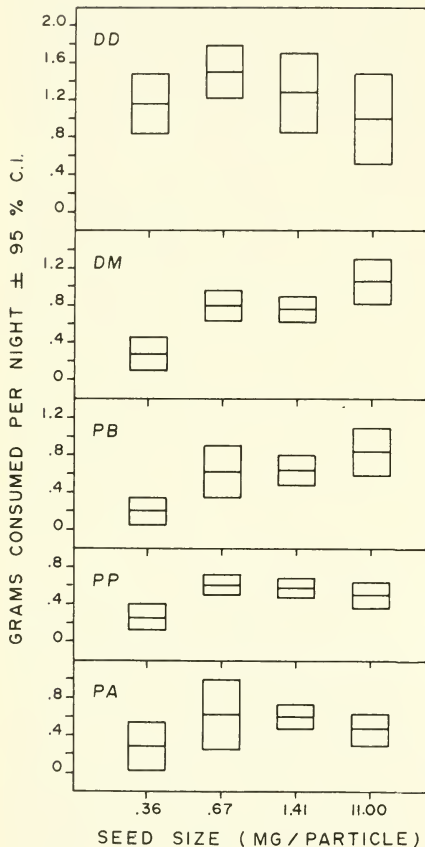


Fig. 3 continued.

B. Results of an experiment identical to that described above, but with smaller seed size classes and samples of ten runs per species. Again, the significant interspecific differences in consumption (Wilks' $L = .040$; $F_{16,55} = 6.50$, $P < .0001$) are largely due to the fact that large animals ate more of all sizes ($\lambda = 8.0$), with a minor difference ($\lambda = 1.8$) due to variation in the extent to which the smallest seeds are avoided. Note again that there is no tendency for larger species to prefer large seeds.

whether we should expect larger or smaller animals to specialize to the greater extent on profitable patches. Nevertheless, it appears from the model that body size may influence aspects of foraging behavior far more subtle than seed size choice alone. Some laboratory

studies offer tentative support for this idea. Several authors (Reichman and Oberstein 1977, Price 1978a, Hutto 1978; but see Trombulak and Kenagy 1980) have observed differences between large and small heteromyids in use of seeds that occur in different local densities; the larger species specialize to a greater extent on dense seed aggregations. In contrast, the few studies of seed patch selection in the field provide no evidence that large species specialize on clumped seeds (Frye and Rosenzweig 1980, Price unpublished). This latter result may be an artifact of using millet sprinkled on the soil surface as bait. A single millet seed is five times larger than most naturally occurring seeds (cf. Reichman 1976) and may be perceived by all heteromyids as a "profitable patch." Indeed, movement patterns of heteromyids exploiting natural seed resources are consistent with the hypothesis that larger species use more widely spaced, rich patches (Bowers 1982). This discrepancy between conclusions drawn from baiting experiments and those based on observation of natural movement patterns underscores the great need for field experiments that mimic more accurately what heteromyids are encountering in nature.

Coexisting heteromyids differ not just in size, but also in morphological traits that are linked to the gait used in rapid locomotion. Reichman (1981) developed a graphical model that considers whether gait should influence seed patch choice. The model assumed that bipedal animals have lower energy expenditure at high speed than quadrupedal animals of similar size. This assumption leads to the expectation that bipedal forms should specialize to a greater extent than quadrupedal forms on clumped, widely spaced seed resources. Because bipedal heteromyid species are larger on average than quadrupedal species, Reichman's conclusions supplement those of Price (1981, 1982a). Recently, however, Thompson (1982c) and Thompson et al. (1980) have called into question the assumption that bipedal locomotion is more efficient than quadrupedal locomotion at high speeds. Their results suggest that the leveling-off of metabolic expenditure at high velocity reported by Dawson and Taylor (1973) and Dawson (1976) for bipedal animals may be a methodological artifact, and

that there are no obvious differences in metabolic rate between quadrupeds and bipeds traveling at the same speed. This finding does not, however, preclude the possibility that something more subtle is going on. Hoyt and Taylor (1981) were able to show that the relationship between metabolic rate and travel velocity is not linear within a gait, and that animals choose to travel at certain speeds because of this nonlinearity. If quadrupedal and bipedal animals have different preferred speeds, then there could be a real difference in their efficiency of travel that would be difficult to detect by measuring oxygen consumption of animals on a treadmill.

We conclude from these preliminary observations that morphological differences among coexisting heteromyids are likely to be associated with differences in the efficiency with which various seed resources can be harvested, and consequently with differences in resource use in nature. Exactly what form resource partitioning takes, though, is still in question. The diet data reviewed earlier suggest that direct partitioning of seeds on the basis of some intrinsic property such as size, nutritional quality, or husking difficulty is not sufficient to account for observed patterns of coexistence.

The conspicuous differences in microhabitat affinity among coexisting species could represent an indirect partitioning of seeds by differential patch choice if microhabitats differ in the seeds they contain or in the methods that must be used to harvest them. Detailed comparison of the seed reserves in different microhabitats has just begun, but preliminary results suggest substantial variation. Several workers have noted that average seed density in standard surface soil samples is higher under the canopy of shrubs than in open spaces between shrubs (cf. Goodall and Morgan 1974, Nelson and Chew 1977, Thompson 1982b). Furthermore, Reichman and Oberstein (1977) and Reichman (1981), working in the Sonoran Desert, found that the coefficient of variation in seed density is much higher for samples taken in open spaces than for those taken under shrubs. This suggests that seeds are more clumped in open spaces. Preliminary data from another Sonoran Desert site (Price and Reichman, unpublished) extend these findings

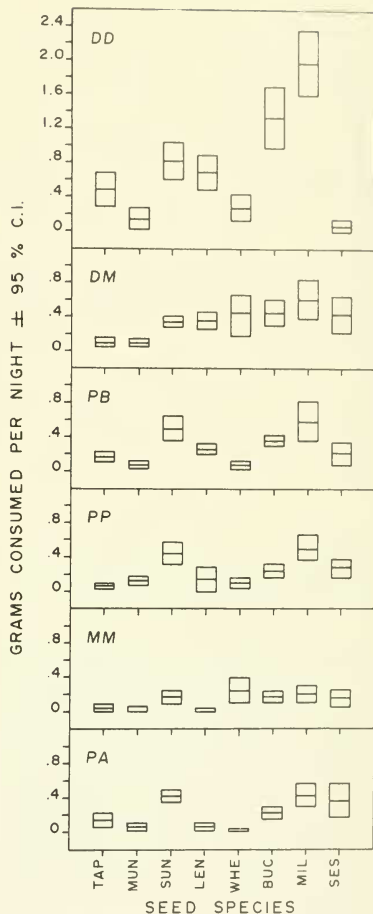


Fig. 3 continued.

C. Results of an experiment similar to those described above, except that animals were presented with equal weights of eight commercially available seed species that differ substantially in nutritional value. (TAP = tapioca; MUN = mung; SUN = sunflower; LEN = lentil; WHE = wheat; BUC = buckwheat; MIL = millet; SES = sesame). There were 14 runs per species. As before, significant differences between species in consumption (Wilks' $L = .010$; $F_{40,181} = 8.67$; $P < .0001$) are primarily those related to the effect of body size on consumption of preferred seeds ($\lambda = 25.5$). In general, preferences were similar across species, with sunflower, millet, and buckwheat taken most often. There was some variation in ranking of wheat and sesame ($\lambda = .86$), but this seems unrelated to body size or taxonomic similarity.

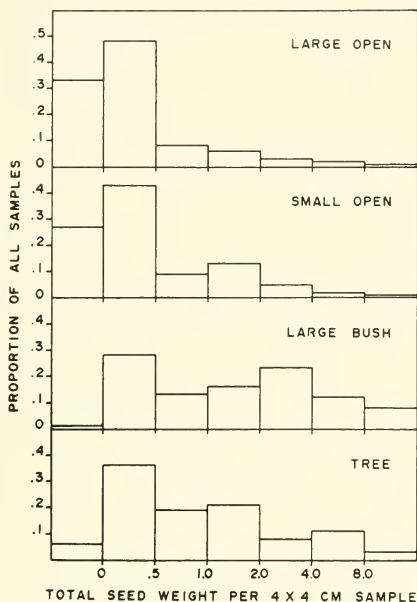


Fig. 4. Characteristics of seeds extracted from 160 4×4 cm soil samples taken in August 1980 from each of four microhabitats at the Santa Rita Experimental Range near Tucson, Arizona. Refer to Price (1978b) for a description of the study site and microhabitats, and to Reichman and Oberstein (1977) for a description of seed extraction techniques.

A. Distribution of total weights of seed (in mg) extracted per sample from Large Open, Small Open, Large Bush, and Tree microhabitats. There is significant heterogeneity among microhabitats in seed abundance ($G = 191$, d.f. = 18, $P < .005$), which is primarily due to differences between open and vegetated microhabitats (Large and Small Open form a homogeneous subset, as do Large Bush and Tree).

(Fig. 4) by indicating that microhabitats differ not only in seed abundance but also in the species of seed they contain and in the density and particle size of the soil matrix from which the seeds must be extracted. Soil under shrubs and trees contains much organic debris of about the same density and particle size as seeds. This could easily influence the method that must be used to separate seeds from the soil matrix. (It certainly influences the efficiency with which humans can extract seeds from soil samples!) Although it is intriguing that *D. merriami* prefers clumped

seeds in the laboratory and also forages in open spaces, which appear to contain the most clumped seeds, we cannot yet be certain that any of these differences between microhabitats influence heteromyid harvest efficiencies or foraging choices; Price and her collaborators are currently studying foraging behavior in the laboratory and field to see whether this is the case.

Despite the fact that we are not certain that adaptations for efficient seed harvest are ultimately responsible for microhabitat affinities, there is good experimental evidence that interspecific differences in microhabitat use are sensitive to the presence of coexisting heteromyid species. Price (1978b) and Wondolleck (1978) observed expansion and contraction in the array of microhabitats used by heteromyids when potential competitor species were experimentally removed or added, respectively. These results suggest that microhabitat specialization would diminish substantially under pressure of intraspecific competition if interspecific competitors were removed permanently from an area (cf. Colwell and Fuentes 1975), and they further implicate competitive interactions as a major cause for microhabitat preferences. The possibility remains, however, that experimental changes in rodent densities in some way induced changes in predator density or behavior, and that the indirect effects of the experiments on predators were responsible for microhabitat shifts. We think this is unlikely, especially since the smallest pocket mouse species with the most generalized morphology was the one that most heavily used open spaces (presumably the "riskiest" microhabitat) following removal of *Dipodomys merriami* in both sets of experiments. Nevertheless, we hope experiments like those of Price and Wondolleck will be repeated with appropriate controls for effects of predation.

In summary, we have reviewed evidence that coexisting heteromyid rodents compete for limited seed resources; that differences in body size and shape appear to be associated with some differences in foraging behavior and abilities; that microhabitat use is sensitive to the presence of competitor species; that microhabitats appear to contain different seed resources; and that heteromyids may prefer the types of seeds that are contained

in the microhabitats they use in nature. All of these observations are consistent with the hypothesis that competition has played a major role in the evolution of two salient features of heteromyid communities: divergence between coexisting species in microhabitat affinities and in body size and shape.

SYNTHESIS AND PROSPECTUS

Communities of seed-eating desert rodents in North America have received such intensive study, especially in the last decade or so, that they are understood better than most other terrestrial vertebrate systems. As a consequence, current views of how communities in general are organized are influenced strongly by the perspectives taken by ecologists who work on desert rodents. This makes it imperative that we evaluate critically what is and is not known about this model system. In the remainder of this paper we outline a way of viewing communities that integrates the divergent perspectives that have been taken by desert rodent ecologists and suggests a general direction for further research.

As we have indicated in this review, a salient characteristic of heteromyid communities is that coexisting species differ in morphology and in microhabitat affinity. Few mammalogists would argue with this statement; indeed, it appears applicable to vertebrate communities in general. Most debate has focused not on the existence of these patterns, but instead on the nature of the causal mechanisms and the way that those determine the number and kinds of species that coexist in habitats of varying structure and productivity. There has been a tendency to treat different explanations as alternative, mutually exclusive hypotheses, with the implication that accepting one means rejecting the others. Traditionally, there have been two basic points of view. One emphasizes the importance of predation as a selective agent that has molded the evolution of heteromyid morphology, behavior, and community structure. The other emphasizes the importance of food scarcity caused by an unpredictable environment and the foraging activities of competitors.

These traditional "one-factor" perspectives naively assume that characteristics of animals

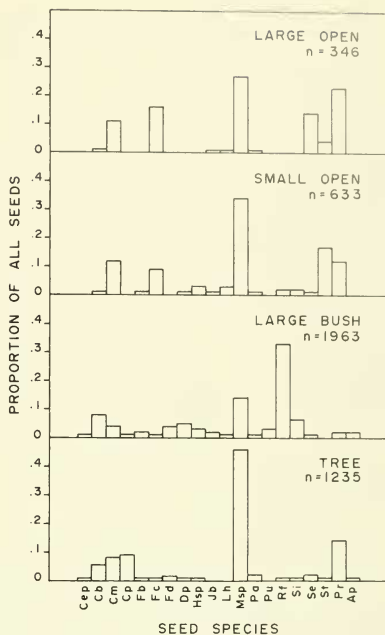


Fig. 4 continued.

B. Species composition of seeds extracted from different microhabitats. The proportional abundances of the 20 most common seed species are indicated, along with total numbers of seeds extracted (n). Again, there is significant overall heterogeneity among microhabitats in seed species composition ($G = 6023$, d.f. = 75, $P < .005$). Large Open and Small Open form a homogeneous subset that is different from Large Bush or Tree, each of which is different from all others. These data indicate that microhabitats differ not only in amounts, but also in species, of seed they contain. Cp = *Celtis pallida*; Cb = *Cryptantha barbigera*; Cm = *C. micrantha*; Cp = *C. pterocarpa*; Fb = "faceted ball"; Fc = *Filago californica*; Fd = "flat disk"; Dp = *Daucus pusillus*; Hsp = *Haplopappus* sp.; Jb = "jelly banana"; Lh = *Lotus humistratus*; Msp = *Mollugo* sp.; Pa = "Panicum"; Pu = "pumpkin"; Rf = "reticulate football"; Si = "Sisymbrium"; Se = *Spermeopsis echinata*; St = "strawberry"; Pr = *Pectocarya recurvata*; Ap = "Apium".

evolve in response to one overwhelmingly important selective force, and that, once an important force has been identified, the system has been understood. It must instead be the case that the behavior and morphology of an animal represent an integrated response to the diverse array of environmental factors that determine fitness. Therefore we feel that

the relevant question to address is not Which factor has been the most important? but instead What has been the role of each factor in producing the patterns we see? By adopting the broader perspective implicit in the second question, we reduce the risk of interpreting rodent communities simplistically in terms only of the factors we can study conveniently. To date, for example, there is little evidence that predation has had a significant effect on heteromyid community structure. We would be wrong, however, to conclude from this that competition is the only factor we need consider to account fully for characteristics of these communities. The apparently overwhelming importance of competition is probably more a function of the ease with which one can manipulate food, habitat structure, and competitor density; and the difficulty of manipulating predation risk, than a reflection of the true importance of competition relative to predation.

A number of approaches can be used to investigate the basis for particular community-level patterns. One that has been used extensively is analysis of the patterns themselves. In this approach the expected consequences of various factors for patterns of morphology or resource use are developed and compared with those exhibited by real communities. If two factors yield different expected patterns, then in principle one can be rejected (for example, see Price 1982b, Strong et al. 1979). Major problems with pattern analysis are that unambiguous expectations are often difficult to derive, and that very different factors often yield similar expectations.

Direct experimental manipulation is an alternative approach that has obvious virtues, but several disadvantages as well. First, it is often difficult to set up an appropriate and effective manipulation. For example, to determine the relative importance of predation directly, one must be able to manipulate it; and this is notoriously difficult to do in some terrestrial systems. Second, if there is no response to a manipulation, one often doesn't know why. The factor could indeed be important, but it is also possible that the manipulation was too small in scope to elicit a measurable response, or that for one reason or another the system simply lacks the capacity to respond.

A third approach is to use detailed analysis of the behavior of individuals as a vehicle for developing testable predictions about the properties of populations and communities (Pulliam 1976, Werner and Mittelbach 1981). Because this "microecological" approach has not yet been applied to heteromyid rodent communities, we will elaborate here on the method.

Consider the individual heteromyid rodent. To achieve genetic representation in future generations, it must be able to find sufficient energy and materials to grow, maintain itself, and reproduce in an environment characterized by low water availability and high diurnal and seasonal temperature fluctuations—and to avoid being eaten while acquiring energy and mates. The question of the relative importance of different factors for salient features of heteromyid community organization resolves itself into two questions at the individual level: (1) How is microhabitat choice influenced by relative harvest profitability, physiological cost, and predation risk? (2) How does the morphology of an individual influence its ability to harvest seeds and avoid predators in particular microhabitats?

The simplest way to attack these "microecological" questions is to use optimal foraging theory as a tool to derive predictions about how the microhabitat choice of morphologically distinct species ought to vary if individuals forage so as to maximize net rate of energy intake. By comparing observed with expected behaviors, one can ascertain whether constraints other than those of harvest efficiency (such as predator avoidance) must be incorporated into foraging models to explain the observed microhabitat choices of different rodent species. Of course, this approach is useful in distinguishing the relative importance of different constraints only if they yield different predicted optimal behaviors. If an animal behaving so as to minimize predation risk is predicted to behave in the same manner as one maximizing seed harvest rates, then this approach has no power in discriminating between two very different models of behavior. In general, however, we expect this will not be a problem, because it seems unlikely that the most profitable patches from a harvest efficiency point of

view will consistently be the least risky as well.

Developing predictions about optimal microhabitat selection is tedious, but straightforward because the theory is well developed (cf. Pyke et al. 1977, Werner and Mittelbach 1981). To apply it one needs to estimate known model parameters, such as how the seed resources contained in one microhabitat differ from those contained in another, how the expected net rate of energy harvest by an individual varies between microhabitats, and how morphology influences these foraging parameters. Armed with this knowledge, one can predict microhabitat preferences under natural or experimentally manipulated conditions, and test the predictions. If patterns of microhabitat use conform to those predicted, then it is in principle possible to develop testable models of niche relationships and competitive interactions between species based on the assumption that interactions are solely exploitative in nature (cf. MacArthur 1972, Pulliam 1976). The power of this approach lies in its ability to generate simple testable models of community structure whose assumptions and predictions are explicitly stated. If the model does not yield accurate predictions, then the assumptions about what constraints influence behavior or population dynamics must be wrong. Even if the model is wrong, progress in understanding nature has been made, for one knows that the next step is to modify the model so as to incorporate different assumptions, and test the new predictions. For examples and further discussion of these points, see Mittelbach (1981), Werner and Mittelbach (1981), and Sih (1980, 1982).

A major advantage of the microecological approach is that one can use it to detect the effects of factors like predation without having to manipulate predator populations directly in the field. A major disadvantage is that, although it is possible in principle to build models of communities from knowledge of individual behavior, in practice the number of variables one would have to incorporate into realistic behavioral models becomes so large that the approach may turn out to be unwieldy. Consider foraging behavior, for example. Microecological analyses may eventually enable us to understand and

thus to predict how individual rodents respond to specified conditions, such as habitats with certain physical structure, patterns of food availability, and different kinds of predators. Unfortunately, however, these conditions themselves probably are not constants in nature, but instead are variables that are influenced by a wide variety of factors. The short- and long-term availability of food should depend in part on the foraging activities of intraspecific and interspecific competitors and the way these affect spatial distributions and recruitment in food plant populations. Similarly, the kinds of predators present will be affected by the other conspecific and heterospecific prey present in an area, and the predators in turn may influence the abundance and distribution of prey populations, thus affecting their interactions. If these sorts of complex feedbacks are important in the organization of desert rodent communities—and we suspect that they are—then they may be more easily detected and understood by macroecological experimental manipulations than microecological ones. For example, a recent experiment in which we added modest quantities of millet seeds to large areas of Chihuahuan desert habitat (Brown and Munger, in preparation) gave the interesting result that *Dipodomys spectabilis* increased in density and *D. merriami* and *D. ordii* decreased. Apparently the decline of the two smaller kangaroo rat species was a consequence of interference or exploitative competition from the larger *D. spectabilis*. This response would have been difficult to anticipate from microecological approaches, because all three *Dipodomys* species should have experienced increased foraging success after the manipulation.

All of this points out the limitations of our present knowledge and the need for additional research of many kinds. As much as we have learned about desert rodent communities in the last decade or two, we have only scratched the surface. Perhaps we have reached the stage where sufficient background work has been done to describe many of the important patterns of community organization and to suggest mechanistic hypotheses to account for these patterns. Clearly much imaginative work and many different approaches can contribute to testing these hypotheses.

ACKNOWLEDGMENTS

A great many people who share interests in desert rodents have helped to develop the ideas presented here. We wish to thank especially our spouses, colleagues, and students for much intellectual stimulation; N. M. Wasser and an anonymous reviewer for helpful editorial suggestions; and K. Kramer, K. Heinz, J. Munger, D. Thompson, and N. Young for indispensable help. This research has been supported by an NSF Doctoral Dissertation Improvement Grant, NSF Grant DEB 80-22164, Sigma Xi and University of California, Riverside, Intramural and Faculty Development awards to MVP, and NSF grants (most recently DEB 80-21535) to JHB.

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